

SOME NEW TYPES OF CHROMOSOME DISTRIBUTION AND THEIR RELATION TO SEX

FERNANDUS PAYNE

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY
IN THE FACULTY OF PURE SCIENCE
COLUMBIA UNIVERSITY

[Reprinted from BIOLOGICAL BULLETIN, Vol. XVI., Nos. 3 and 4, February and March, 1909.]



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FERNANDUS PAYNE.

INTRODUCTION.

Since the discovery of the "accessory chromosome" in *Pyrrhocoris*, by Henking, this chromosome or its equivalent has been described in many other Hemiptera (Paulmier, Montgomery, Wilson and others) and also in many other tracheates—Orthoptera (McClung, Sutton and others), Coleoptera (Stevens), Myriapoda (Blackman and Medes) and Odonata (Lefevre and McGill). Wallace and Berry have also described it in the Arachnida. Essentially, the "accessory chromosome" is a spermatogonial chromosome, which is without a synaptic mate, and which divides in but one maturation division. The end result is that one half of the spermatozoa receive one more chromosome than the other half. The spermatozoa are therefore dimorphic in respect to the number of chromosomes.

A second type of dimorphism of the spermatozoa was discovered by Stevens ('05) in *Tenebrio* and by Wilson ('05) in *Lygaeus*, *Cænus* and several other genera of Hemiptera, and was afterward found by Stevens ('08) in the Diptera. In this type, both classes have the same number of chromosomes, but differ in that one class contains a large idiochromosome and the other a small one. These observers showed that the class containing

¹ My material was taken in large part by Professor E. B. Wilson on his collecting trip through the South and West, and it is due to this material that I have been able to make this comparative study. I have also received much valuable material from Rev. A. H. Manee, Southern Pines, N. C., besides collections which I have made in New Jersey, Massachusetts and Indiana. This material Mr. E. P. Van Duzee, of Buffalo, has kindly identified for me. Throughout the entire work, I have been much indebted to Professor Wilson for helpful suggestions and criticisms. I wish to thank Dr. Alexander Petrunkevitch for the privilege of working in his private laboratory at Short Hills, New Jersey, for five weeks during the spring of 1908. The U. S. Bureau of Fisheries also extended to me the privilege of working in the laboratory at Woods Hole, Massachusetts, during the summer of 1908.

the small idiochromosome produces males and the other class females. Wilson likewise established the fact that in forms having an accessory chromosome, the spermatozoa that contain this chromosome are female-producing, the others male-producing. In respect to sex-production, the accessory chromosome is, therefore, identical with the large idiochromosome. The homologue of the small idiochromosome is lacking.

The relation of the accessory chromosome to sex-production has been confirmed by the work of Montgomery ('06) on the Hemiptera heteroptera, of Stevens ('05 and '06) in the Coleoptera, of Boring ('07) on the Hemiptera homoptera, of Lefevre and McGill ('08) on *Anasa* and *Anax* (one of the Odonata), and of Wassilieff ('07) on the cockroach. It has also received confirmation in the recent work of Morgan ('08) and von Baehr ('08) in the parthenogenetic reproduction of *Phylloxera* and *Aphis*.

Wilson ('09) has described a third type in *Syromastes*. Gross ('04) showed that the accessory chromosome in this species is bivalent, but described and figured 22 chromosomes in both male and female cells. Wilson confirmed this for the male, but inferred that the female cells should contain 24 chromosomes or two more than the male, and he has since confirmed the correctness of this inference by direct observation. Hence, contrary to the assumption of Gross, both classes of spermatozoa must be functional, the class containing the bivalent accessory chromosome producing females, the others, males.

A fourth type was described by myself ('08) in a preliminary note on *Gelastocoris* (*Galgulus*). In this type there are five chromosomes which divide as univalents in the first maturation division. In the second division they do not divide, but four of the five pass to one pole and the other one to the opposite pole. In this form the female has three more chromosomes than the male, and the spermatozoa which contain the three extra chromosomes must therefore be the female-producing class.

A study of the Reduviidæ has brought to light several additional types here to be described. In *Diplocodus*, belonging to this family, occurs the second type with one large and one small idiochromosome. As in *Lygæus* and other forms, these divide

as univalents in the first division, but in the second, they come together in the middle of the metaphase plate to form a dyad. The two chromosomes of this dyad group separate, one passing to one pole and the other to the opposite pole.

Another and the first new type described in the present paper is found in *Fitchia*, where there are three chromosomes which divide as univalents in the first division, but in the second division arrange themselves in the form of a triad group, two members of which pass to one pole and one to the other.

In *Prionidus* and *Sinea*, we find a second new type in which there are four corresponding chromosomes. These four divide only in the first division. In the second, they are arranged in the form of a tetrad group, three members of which pass to one pole and one to the opposite one.

A third new type is present in *Acholla multispinosa*. Here there are six univalent chromosomes in the first division. My evidence is not absolutely conclusive in this case, but as far as it goes, it indicates that these six divide in the first division, but in the second, five of them pass, without dividing, to one pole and one to the other.

In all these cases the male and female chromosome groups differ correspondingly. In *Diplocodus* the male and female cells have the same number of chromosomes, but differ in that the female cells have a large idiochromosome and the male cells a small one. In *Fitchia*, the female has one more chromosome than the male; in *Prionidus* and *Sinea* two; in *Gelastocoris* three; and in *Acholla multispinosa* four. These facts prove that in each case one class of spermatozoa is female-producing and the other class male-producing.

The discovery of these types adds nothing new in principle to the theory of sex production as put forward by Wilson ('06), but they are perfectly consistent with it. *Acholla multispinosa*, in which the male seems to have the larger quantity, offers evidence against the interpretation that sex is determined by a quantitative relation of the chromatin.

In the preliminary note ('08) on *Gelastocoris*, I used the term "differential chromosomes" to refer to the chromosomes of the pentad group. Throughout the present paper, the same term

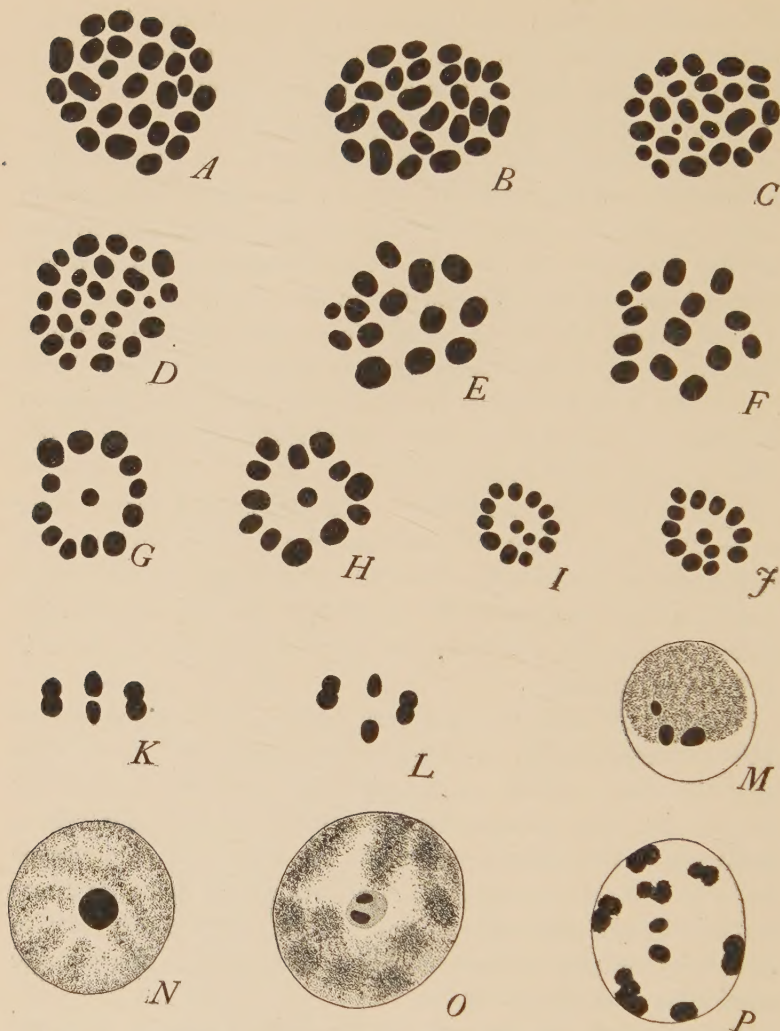


FIG. 1. *Diplocodus exsanguis* Stal. A and B, metaphase, polar view, of two female cells showing 26 chromosomes; C and D, metaphase, polar view, of two male cells, 26 chromosomes; E and F, two metaphase figures of the first maturation division, 14 chromosomes; G and H, two metaphase figures of the second maturation division, 13 chromosomes; I and J, two anaphases of the second division, taken from the same spindle; K, a side view of the second division, metaphase; L, side view of the second division, early anaphase, showing the early separation of the idiochromosomes; M, the early growth period, about contraction-phase. Two of the dark bodies are probably the idiochromosomes and the other the plasmosome; N and O, two drawings from approximately the same stage in the growth period. In N the plas-

will be used in reference to the chromosomes of the triad, tetrad, pentad and hexad groups.

DESCRIPTIVE.

Diplocodus ersanguis Stal.

In *Diplocodus* we find a typical pair of idiochromosomes as described by Wilson ('05) for several species of Hemiptera. A description is included here mainly to show the range of variability in chromosome distribution found within the limits of a single family of Hemiptera. There are 26 chromosomes in the somatic groups of both male and female cells (Fig. 1, *A*, *B*, *C* and *D*). While there is very little difference in size in the idiochromosomes, there is one chromosome in the male group, noticeably smaller than the others, which without doubt, is the small idiochromosome. As the idiochromosomes are separate in the first division, the metaphase plate of the first division shows 14 chromosomes (Fig. 1, *E* and *F*), one more than half the spermatogonial number. In these figures, the small idiochromosome can be readily identified, but one cannot always be sure of the large one. Both divide in this division. In the second division, there is a rearrangement of the chromosomes, 12 taking up the position of a ring with the idiochromosomes, one above the other, in the center (Fig. 1, *I* and *J*, side views of the second division, metaphase). A polar view of the metaphase accordingly shows only 13 chromosomes. Wilson figures them as coming into close apposition at this time to form an asymmetrical dyad. While I have not examined a large number of cases in *Diplocodus*, they, here, seem not to fuse, but only to come very close together as shown in Fig. 1, *I*. Fig. 1, *J*, shows that their separation precedes the division of the chromosomes in the ring, as is also the case in the forms described by Wilson. Fig. 1, *K* and *L*, represent two anaphases taken from the same spindle.

The history of the idiochromosomes during the growth period has not been fully traced. In the contraction-phase (Fig. 1, *M*), mosome stains intensely black, while in *O* it is pale and the idiochromosomes can be seen lying embedded in it; *P* is a prophase figure of the first division, showing the idiochromosomes in marked contrast to the looser masses of chromatin condensing to form the remaining chromosomes. The enlargement is 3,726 diameters.

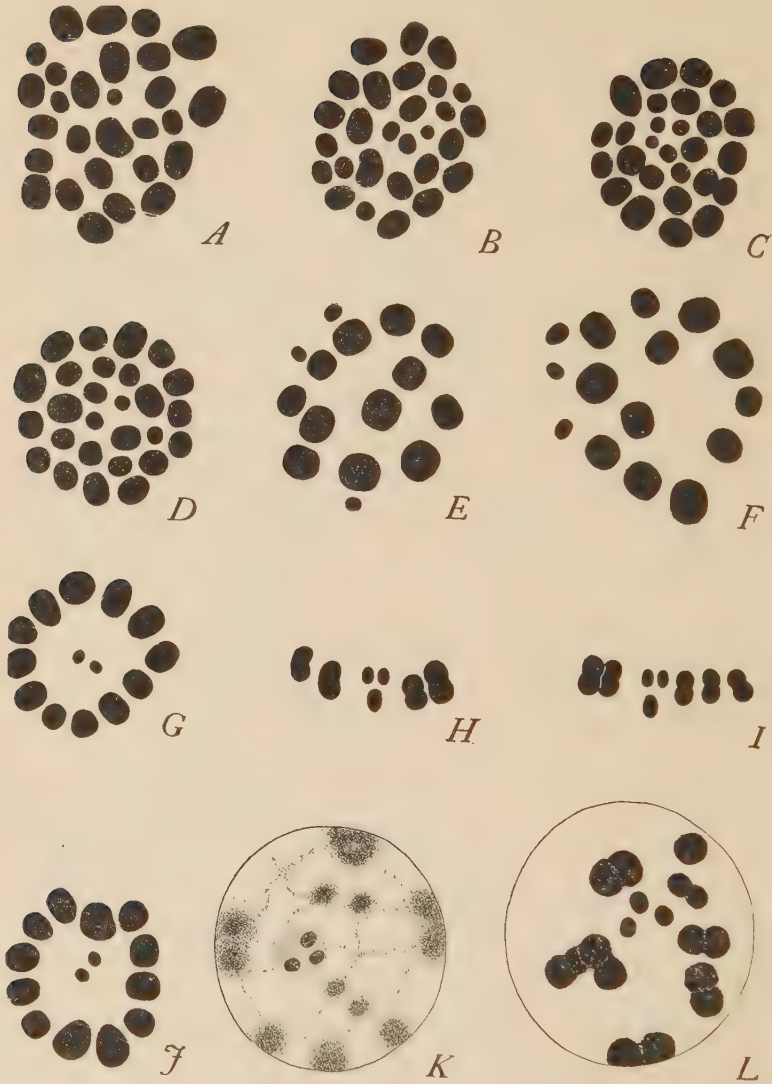


FIG. 2. *Fitchia spinosula* Stal. *A* and *B*, two female cells, metaphase, polar view, 28 chromosomes; *C* and *D*, two male cells, metaphase, 27 chromosomes; *E* and *F*, first maturation division, metaphase, showing 15 chromosomes—the three smallest ones are the differential chromosomes; *G* and *J*, polar views of the second division, metaphase—only two of the differential chromosomes are shown, as the third lies beneath these two; *H* and *I*, side views of the second division, metaphase—the triad group, formed by the three differential chromosomes, in the center; *K* gives the typical appearance of the plasmosome and differential chromosomes during the greater part of the growth

three dark bodies are sometimes present. Judging from the conditions found in Fig. 1, *N* and *O*, and from the relation of the chromosomes and plasmosome in *Prionidus*, where it has been fully worked out, it seems very probable that two of these dark bodies may be the idiochromosomes and the other, the plasmosome. Fig. 1, *N* and *O*, represent about the same stage in the growth period, but are entirely different in appearance. In *N*, the whole nucleolus stains intensely black, but again as shown in *O*, we see a pale plasmosome with the idiochromosomes embedded in it. There is no doubt but that the nucleolus in both cases represents the same thing. The only difference is in the staining capacity of the plasmosome. What causes this difference is impossible to say. However, it is very probable that the plasmosome is an active agent and as such is constantly undergoing changes, either chemical or physical, or both. In the prophase of the first division (Fig. 1, *P*) the plasmosome breaks down and the idiochromosomes stand out plainly while the other chromosomes are condensing. In the cases described by Wilson ('05) the idiochromosomes were attached to a plasmosome and not actually embedded in it as we find in *Diplocodus*.

Fitchia spinosula Stal.

In forms where the accessory chromosome is a single unpaired element, this chromosome remains throughout the growth period as a chromosome nucleolus, and since it divides in but one maturation mitosis, half the spermatozoa receive one more chromosome than the other. As already stated, these spermatozoa produce females, the others males, since the female somatic cells contain one more chromosome than the male.

In *Fitchia*, an exactly similar result is produced, yet, the manner in which the unequal distribution is brought about is entirely different. The female cells (Fig. 2, *A* and *B*) have 28 chromosomes, and the male cells (Fig. 2, *C* and *D*), 27. In neither of these groups can the differential chromosomes be recognized with certainty. The first division (Fig. 2, *E* and *F*) shows 15

period; *L*, prophase of the first maturation division—the plasmosome has disappeared and the chromosomes are forming. The enlargement is 3,726 diameters.

chromosomes, three of which are much smaller than the others, and prove to be the univalent differential chromosomes. Here they lie on the periphery. All the chromosomes divide equally as the same total number (15) is found in the metaphase plate of the second division. Now, however, the arrangement is different, the 12 larger chromosomes forming an irregular ring within which lie the three differential chromosomes in the form of a triad group, similar in arrangement to the pentad group in *Gelastocoris* (*Galgulus*). Two of these three, nearly or quite of the same size, lie in the same plane, while the third, which is a little larger, lies either above or below them on the other side of the equatorial plane (Fig. 2, *I* and *J*, two side views of the second division, metaphase). While my material does not show the anaphases of this division, the relations in the male and female cells and a comparison between this and the other two species, which show the same type of distribution and where anaphases are present, leave little doubt as to the manner of division. The 12 chromosomes in the ring divide equally, while the members of the triad group do not divide individually, but the group as a whole separates so that the two chromosomes pass to one pole and the one to the other. Two classes of spermatozoa containing respectively 13 and 14 chromosomes are thus produced. Since the female number is 28 and the male 27, it is evident that the reduced number in the egg must be 14, and that females are produced upon fertilization of the egg by the 14-chromosome class; males upon fertilization by the 13-chromosome class, as follows:

Egg 14 plus spermatozoön 13 = 27 (♂),

Egg 14 plus spermatozoön 14 = 28 (♀).

Although the end result is the same as in those species with an odd chromosome, this gives us a new type of chromosome distribution, which is the first step in a series, which bridges the gap between the relations found in *Diplocodus*, on the one hand, and *Gelastocoris* (*Galgulus*) on the other.

The history of the differential chromosomes in the growth period has not been followed in detail, but during the greater part of this time, a pale plasmosome is present and embedded

in it are the three differential chromosomes as densely staining compact bodies (Fig. 2, *K*). In the prophase of the first division, the plasmosome disappears and the differential chromosomes remain (Fig. 2, *L*).

Rocconota annulicornis Stal.

With the exception of the size relations of the differential chromosomes, we find practically the same conditions in this form as in *Fitchia*. The spermatogonial cells (Fig. 3, *A* and *B*) show 27 chromosomes. Unfortunately no good female groups were present in my material, but since the relations are so similar to those found in *Fitchia*, there seems little doubt but that it contains one more chromosome than the male. In the first division, metaphase plate (Fig. 3, *C* and *D*), are 15 chromosomes, three of which are distinctly smaller than the remaining twelve, and which prove to be the differential chromosomes. All divide equally in this division. The characteristic regrouping in the second division again occurs. The 12 larger chromosomes form an irregular ring with the triad group, made up of the three differential chromosomes in the center (Fig. 3, *G* and *H*, side views of the second division, metaphase). Here all three differential chromosomes are practically of the same size. The chromosomes in the ring divide equally, while those of the triad group separate as in *Fitchia*, so that two pass to one pole and one to the other. The two classes of spermatozoa thus produced, are essentially similar to those of *Fitchia*, and are respectively male and female producing. Fig. 3, *I* and *J*, are two anaphases taken from the same spindle which show the unequal distribution of the chromosomes, 14 passing to one pole and 13 to the other.

Throughout the growth period, from shortly after synapsis to the prophase of the first division, there is present a distinct pale plasmosome, in which are embedded the three differential chromosomes (Fig. 3, *K* and *L*). The exact stage in which the plasmosome and chromosomes make their appearance could not be determined. Fig. 3, *M*, represents the prophase of the first division, where the plasmosome has disappeared. The differential chromosomes stand out in marked contrast to the looser

masses of chromotin condensing to form the remaining chromosomes.



FIG. 3. *Rocconota annulicornis* Stal. *A* and *B*, male chromosome-groups, 27 chromosomes; *C* and *D*, polar views of the first spermatocyte division, showing 15 chromosomes—the three small ones are the differential chromosomes; *E* and *F*, polar views of the second division—only two of the three differential chromosomes are shown, as the third lies below the two; *G* and *H*, side views of the second division metaphase, showing arrangement of the triad group of differential chromosomes; *I* and *J*, two anaphases of the second division taken from the same spindle, which show the manner of separation of the triad group; *K*, a stage in the early growth period, showing the pale plasmosome and the three differential chromosomes embedded in it; *L*, a stage giving the typical appearance of the nucleus during the greater part of the growth period; *M*, prophase of the first division—the plasmosome has disappeared and the three differential chromosomes are easily recognizable. *K*, *L* and *M* are magnified 2,411 diameters; the remainder 3,726 diameters.

Conorhinus sanguisugus Lec.¹

Conorhinus gives an additional verification of the type described in *Fitchia*. The number and size relations of the chromosomes are somewhat different. The spermatogonial divisions (Fig. 4, *A* and *B*) show 23 chromosomes, two of which are distinctly smaller than the others. In the metaphase plate of the first division (Fig. 4, *C* and *D*) there are 13 chromosomes, ten of which must be bivalent and three univalent as there are 23 in the spermatogonia. In this division, contrary to what is found in all other cases, the bivalent chromosomes form an irregular ring and the differential chromosomes, which are easily recognized by their size relations, take up a central position, but all lie in one plane. All the chromosomes divide equally in this division, so that each secondary spermatocyte receives 13 chromosomes, the arrangement of which is somewhat different from that in the first division. There are ten in the ring, but the differential chromosomes which occupy a central position, show a regrouping as in *Fitchia*. The large and one small one lie in the same plane, but the second small one is either above or below the other two, forming the characteristic triad group (Fig. 4, *G* and *H*, side views of the second division, metaphase). The ten chromosomes in the ring divide equally, while the chromosomes of the triad group separate, two going to one pole and the other to the opposite pole. Fig. 4, *I* and *J*, representing two anaphases from the same spindle, show the chromatin content of the two class of spermatozoa, which contain respectively 13 and 14 chromosomes.

The size relations of the differential chromosomes in the three forms illustrating this type of distribution are different in each case. In *Fitchia* the one which goes to the male-producing pole is slightly larger than the other two. In *Rocconota* all three are practically of the same size and in *Conorhinus*, one of the two which goes to the female-producing pole is larger than the other two.

The history of the differential chromosomes in the growth period has been followed as far as material permits. Sometimes

¹ This identification is somewhat doubtful as all my specimens are immature.

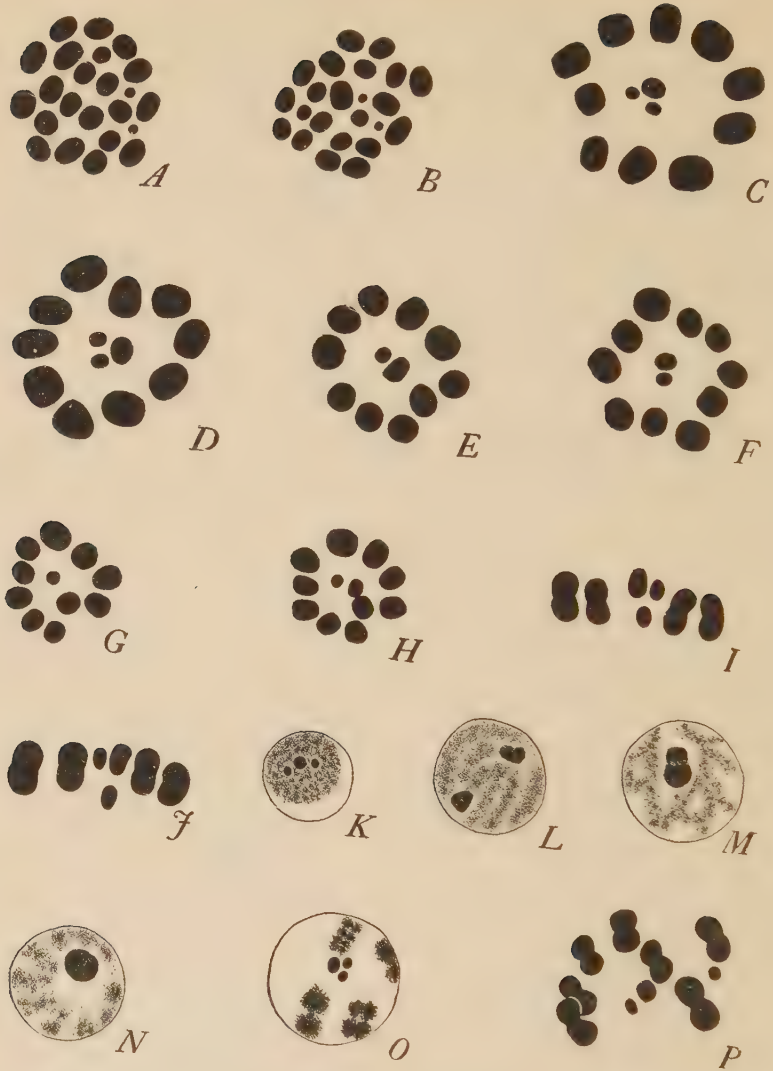


FIG. 4. *Conorhinus sanguisugus* Lec. *A* and *B*, male chromosome-groups, 23 chromosomes; *C* and *D*, polar views of the first maturation division, metaphase—the three differential chromosomes lie in the middle of the irregular ring; *E* and *F*, polar views of the second mitosis—only two differential chromosomes are shown; *G* and *H*, two anaphases of the second division taken from the same spindle and which show the manner in which the triad group separates; *I* and *J*, side views of the second division, metaphase, showing arrangement of the triad group; *K*, a stage in the early growth period, about contraction-phase—the three dark bodies are the three differential chromo-

they appear as separate and distinct individuals in the contraction phase (Fig. 4, *K*). A little later (Fig. 4, *L*) when the chromatin is scattered about through the nucleus, two dark bodies, nearly equal in size, are present. It is very probable that they are both plasmosomes. In one of them, three denser bodies can be faintly, yet unmistakably seen. These are no doubt the three differential chromosomes. The two plasmosomes seem to fuse into one body as in Fig. 4, *M*, and later condense into a somewhat spherical mass (Fig. 4, *N*), which persists throughout the greater part of the growth period. The plasmosome goes to pieces in the prophase of the first division and the differential chromosomes appear at the same time. While in Fig. 4, *M* and *N*, the differential chromosomes cannot be seen, there is little doubt but that they are present in the plasmosome. From these figures alone, it would be impossible to make the above statement, but in view of the condition in *Prionidus*, which is described later, I believe the correct interpretation has been given.

Prionidus cristatus Linn.

In his suggestive papers of '01 and '06, Montgomery described in *Prionidus*, the rest stage of the spermatogonia, the spermatogonial divisions and the rest stage of the primary spermatocytes. For the main part, my observations support his, but as we shall see, he was led to some erroneous conclusions because he did not follow the chromosomes through the first and second divisions. He figures 26 chromosomes in the spermatogonial divisions, and in describing these ('06) he says, "Of the 26 chromosomes two are much larger and two much smaller than the others. All these are found on careful inspection to be arrangeable into a series of pairs, in which the two components

somes; *L*, a stage after synopsis, showing two plasmosomes, in one of which the three differential chromosomes can be faintly seen; *M*, a stage a little later than *L*, showing fusion of the two plasmosomes; *N* shows the complete fusion of the plasmosomes and the typical appearance of the nucleus throughout the growth period; *O*, prophase of the first division—the plasmosome has disappeared—the three densely staining bodies are the differential chromosomes; *P*, a later prophase, just before the chromosomes arrange themselves in the equatorial plate. *K*, *L*, *M*, *N* and *O* are magnified 2,411 diameters; the remainder 3,726 diameters.

of each pair are of approximately equal volume except the two marked *K*, *k*. There is probably no monosome because the number is an even one."

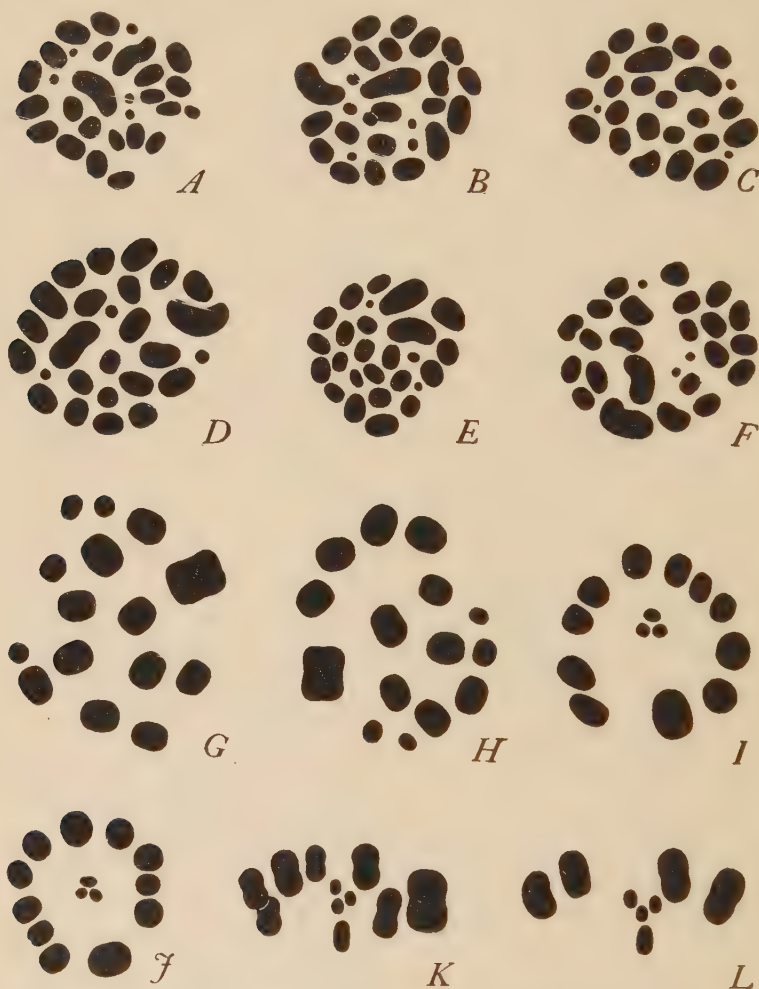


FIG. 5. *Prionidus cristatus* Linn. *A* and *B*, female cells showing 28 chromosomes—the six smallest ones are the differential chromosomes; *C*, *D*, *E* and *F*, male cells, 26 chromosomes—only three of the four differential chromosomes can be recognized with certainty—they are the three smallest ones; *G* and *H*, polar views of the first maturation division, 15 chromosomes—the four smallest ones are the differential chromosomes; *I* and *J*, polar views of the second division, metaphase—only three differential chromosomes are shown; *K* and *L*, side views of the second division, metaphase, showing the arrangement of the tetrad group. The enlargement is 3,726 diameters.

My figures of the male groups (Fig. 5, *C*, *D*, *E* and *F*) agree both in number and in size relations with those of Montgomery. There are 26 chromosomes, two of which are larger and three smaller than the rest. Although Montgomery's figures in both papers ('01 and '06) show three small chromosomes, he describes three small ones in the first paper and only two in the latter. The number of chromosomes and their behavior in the first and second divisions give an explanation of the size relations in the spermatogonia.

The female groups (Fig. 5, *A* and *B*) show 28 chromosomes, six of which are distinctly smaller than the others.

In the first maturation division metaphase, 15 chromosomes are present, four of which can be easily recognized as smaller than the remaining ones and one of the four is decidedly larger than the other three. There is no definite arrangement in these figures. All the chromosomes divide equally, so that accordingly each secondary spermatocyte receives 15 chromosomes, the arrangement of which is entirely different. The eleven larger chromosomes form an irregular ring while the four smaller ones, which prove to be the differential chromosomes, form a tetrad-group in the center (Fig. 5, *K* and *L*, two side views of the second division, metaphase). Unfortunately no anaphases of the second division were present, but the number and size relations in the male and female groups and the analogy between the behavior here and in *Sinea*, which is described later, leave no doubt as to the manner in which the tetrad-group separates. The eleven chromosomes in the ring divide equally, while the members of the tetrad-group do not divide, but the group as a whole separates so that the three smaller ones pass to one pole and the larger one passes to the other pole. Two classes of spermatozoa, containing 12 and 14 chromosomes, respectively, are thus produced. Accordingly the 14-chromosome class contains three small chromosomes while the 12-chromosome class would have none, as the differential chromosome which goes to this pole is as large as one half of one of the smaller dyads (see Fig. 5, *K* and *L*). If the 14-chromosome class meets the egg with 14 chromosomes, three of which are small, we would expect 28 chromosomes in the offspring, six of which should be small.

This number and the size relations are exactly what is found in the female cells (Fig. 5, *A* and *B*). Again, if the 12-chromosome class meets the same egg we would expect 26 chromosomes in the offspring, three of which should be small, and this number and relation is confirmed by the figures of the male cells (Fig. 5, *C*, *D*, *E* and *F*). From the facts at hand, it is evident that the reduced number of chromosomes in the egg is 14 and that three of these are decidedly smaller than the rest. Females must therefore be produced upon fertilization of the egg by the 14-chromosome class of spermatozoa; males by the 12-chromosome class.

Egg 14 plus spermatozoön 12 = 26 (♂),

Egg 14 plus spermatozoön 14 = 28 (♀).

From the above observations, it becomes apparent that the three small chromosomes and one other, which is not recognizable in the spermatogonial divisions, do not pair at synapsis. This gives an explanation of Montgomery's unequal pair.

Prionidus thus gives us a second new type of chromosome distribution and presents the intermediate stage between the types illustrated by *Fitchia* and *Gelastocoris*.

Montgomery has described only the rest stage of the growth period. In his earlier paper ('01) he says: "In the rest stage of the spermatocyte are found four chromatin nucleoli attached to the true nucleolus. One of these is longer than the others and rod-shaped." Later ('06) he describes this stage somewhat differently. "In the complete rest stage of the spermatocytes are found three or four safrininophilous bodies attached to the surface of a large more or less central plasmosome. They are of unequal volumes; and when there are three of them, each appears bipartite, while when there are four, the smallest are each unipartite. Perhaps as in *Sinea*, these relations are to be interpreted as three bivalent diplosomes, the smallest of which may sometimes have its parts separated."

I have followed the history of the differential chromosomes during the growth period somewhat in detail as the material proved favorable for this purpose. Between the last spermatogonial division and synapsis, a pale plasmosome persists. At

the contraction-phase (Plate 1, *A*), there is present in addition to the plasmosome, a deeply staining body, which proves to be the first appearance of the differential chromosomes. In the spireme stage (Plate 1, *B*), shortly after synapsis, the two bodies are present, but the chromatic mass is more spherical. A little later (Plate 1, *C*), the chromatic body has become broken up and a plasmosome has formed around it. The next stage (Plate 1, *D*) shows the two bodies in contact and beginning to fuse. About this time the chromatic mass breaks up for the first time into its constituent elements, the four differential chromosomes, the larger of which is noticeably elongate (Plate 1, *E*). The two plasmosomes fuse completely to form a large more or less spherical one (Plate 1, *F*). Plate 1, *G*, shows the typical appearance of the nucleus throughout the greater part of the growth period. The larger differential chromosome shortens into a somewhat spherical form. All of them lie embedded in the pale plasmosome and not in contact with it as described by Montgomery. Nor do any of them, at any time, show an appearance of being bipartite and their later behavior in the maturation divisions shows conclusively that all four are univalent. As we shall see later, Montgomery's idea as to the relations in *Sinea* were incorrect, and this accounts in part for the wrong interpretation in *Prionidus*. In the prophase of the first division, when the chromatin is beginning to condense to form the chromosomes, the plasmosome disappears and the differential chromosomes remain.

In *Syromastes*, Wilson ('09) describes the same numerical difference in the male and female somatic cells as here described for *Prionidus*. The difference in that case, however, is brought about by two chromosomes which act as a unit and which divide in only one division.

Sinea diadema Fabr.

Montgomery ('01 and '06) described in part the behavior of the chromosomes in a species which he called "*Sinea diadema*," but the relations which I find in this species are entirely different from those which he described. There is, therefore, but little doubt that he studied a different species. This again em-



FIG. 6. *Sineia diadema* Fabr. *A* and *B*, female groups, metaphase figures, showing 30 chromosomes—the six small ones are the differential chromosomes; *C* and *D*, male groups, showing 28 chromosomes—the four small ones are the differential chromosomes; *E* and *F*, polar views of the first maturation division, metaphase, 16 chromosomes—the four small ones are the univalent differential chromosomes; *G* and *H*, polar views of the second division, metaphase—only three differential chromosomes are shown, as the fourth lies below the three; *I* and *J*, side views of the second division, metaphase, showing arrangement of the tetrad group; *K* and *L*, two anaphases of the second division, showing the manner in which the tetrad group separates, and the number of chromosomes in each of the two classes of spermatozoa; *M* gives the typical appearance of the plasmosome and differential chromosomes during the greater part of the growth period; *N*, a prophase of the first division after the plasmosome has disappeared—the four small condensed bodies are the differential chromosomes. *A-L* are magnified 3,726 diameters; *M* and *N* 2,411 diameters.

phasizes the necessity of keeping all specimens for future identification. It seems very probable that the species which Montgomery called "*Sinea diadema*" was *Acholla multispinosa*, for the first maturation division in *Acholla multispinosa* agrees exactly with that which Montgomery figured for *Sinea*.

The behavior of the chromosomes in *Sinea* is practically the same as in *Prionidus* and gives a beautiful confirmation of the results there described. In the female cell (Fig. 6, *A* and *B*), 30 chromosomes are distinctly visible, six of which are much smaller than the others. The male cells (Fig. 6, *C* and *D*) show 28 chromosomes, two less than the female number and four of these are smaller than the rest. There are 16 chromosomes in the metaphase of the first maturation division (Fig. 6, *E* and *F*), and since there are 28 chromosomes in the spermatogonia, 12 of these must be bivalent and four univalent. All the chromosomes divide equally in the first division. Hence the equatorial plate of the second division shows 16 chromosomes, but as usual, their arrangement is different. In the first division, the small chromosomes are peripheral, while in the second, they are central and are arranged in a tetrad-group, as are the four differential chromosomes in *Prionidus*. Fig. 6, *I* and *J*, show two side views of the second division, metaphase, with the tetrad group in the middle. In *Prionidus*, one chromosome of the tetrad group is larger than the other three, while in *Sinea* all four are practically the same size. In the second division, the chromosomes in the ring divide, while the tetrad group separates so that the three chromosomes above go to one pole and the one below to the other. Fig. 6, *K* and *L*, are two anaphases, showing the manner of separation. Two classes of spermatozoa are thus formed, containing 13 and 15 chromosomes, respectively. Judging from these facts, the reduced female group contains 15 chromosomes and females are produced upon fertilization by the 15-chromosome class of spermatozoa; males by the 13-chromosome class.

Egg 15 plus spermatozoön 13 = 28 (♂),

Egg 15 plus spermatozoön 15 = 30 (♀).

The size relations of the differential chromosomes which make

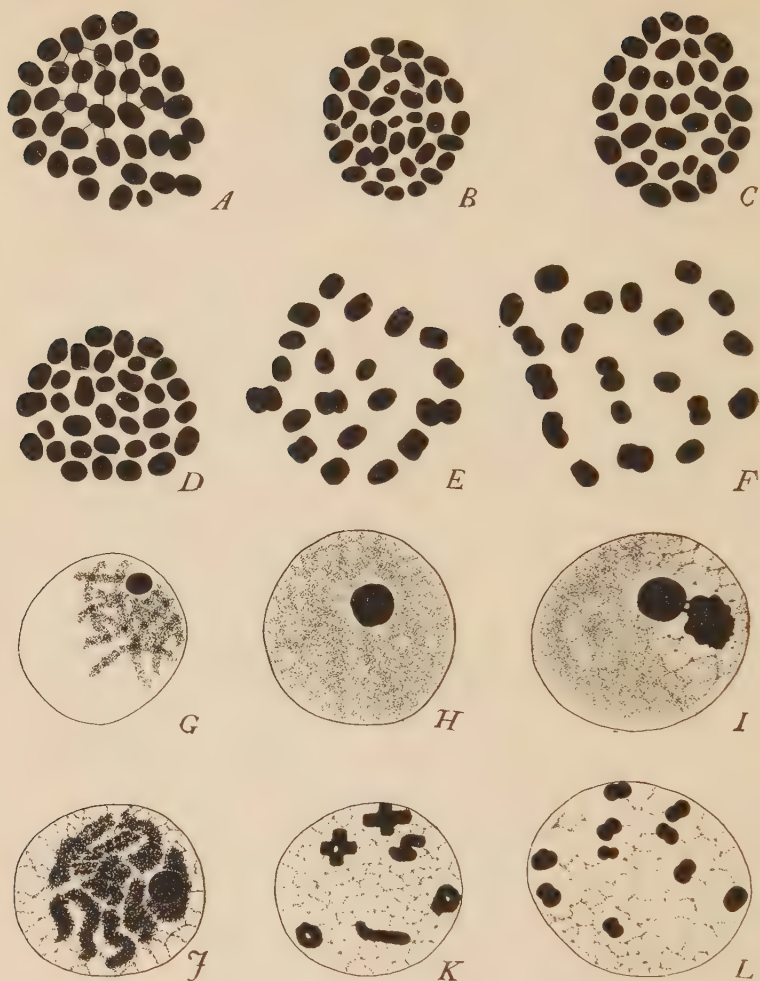


FIG. 7. *Gelastocoris (Galgulus) oculatus* Fabr. *A* and *B*, female groups, metaphase plates, showing 38 chromosomes; *C* and *D*, male groups, showing 35 chromosomes; *E* and *F*, polar views of the first maturation division, metaphase—the differential chromosomes are indistinguishable; *G*, a stage shortly after synapsis, showing the presence of the nucleolus; *H*, typical appearance of the nucleus and nucleolus throughout the growth period; *I*, a very early prophase of the first division—the contents of the nucleolus have been thrown out into the nucleus; *J*, prophase of the first division, when the chromosomes are just beginning to form—the plasmosome is still present, although apparently smaller; *K*, prophase of the first division—the chromosomes are condensing and the plasmosome has disappeared; *L*, late prophase of the first division—the chromosomes are formed, but have not taken up their position in the equatorial plate. *A*, *B*, *C* and *D* are magnified 3,105 diameters; *E* and *F* 2,009 diameters and *G*, *H*, *I*, *J*, *K* and *L* 1,297 diameters.

them easily recognizable in the male and female cells, help to confirm the above statement. Six are present in the female and only four in the male, and this is what we would expect, since one class of spermatozoa has three small chromosomes and other one.

The differential chromosomes have not been followed throughout the entire growth period. Fig. 6, *M*, shows the appearance of the nucleus during the greater part of this period. A large pale plasmosome is present in which are embedded the four differential chromosomes. The condition is almost exactly analogous to that found in *Prionidus*. In the prophase of the first division, the plasmosome disappears and the four differential chromosomes stand out clearly as condensed deeply staining bodies while the other chromosomes are condensing.

Gelastocoris (Galgulus) oculatus Fabr.

In a preliminary note ('08), I described a new type of sexual difference in the chromosome groups of *Gelastocoris oculatus*. At that time my material was limited and some of my conclusions were supported by only a few observations. Since then I have obtained new material and am now in a position to reaffirm all that was stated in the former paper. My figures of the first division showed among the chromosomes one or two minute dark bodies resembling yolk granules. As stated at that time, a doubt might be raised as to whether these bodies were chromosomes. However, my opinion as stated, was supported by the facts that the number of chromosomes in the prophase of the first division before the nuclear wall broke down, was always 20, and that the metaphase plate of the second division invariably showed 20 chromosomes. In my new material, I have found several metaphase plates which show 20 chromosomes without any granules whatever (Fig. 7, *K* and *L*). As the spermatogonial number is 35, 15 of the 20 must be bivalent and five univalent. There is no definite arrangement of the chromosomes in this division, but sometimes 15 are in a more or less irregular ring with the other five in the center, as is shown in Fig. 7, *L*. Whether these five are the same ones which form the pentad group in the second

division is impossible to say. All the chromosomes divide equally so that each secondary spermatocyte receives 20 chromosomes. No reconstruction period follows. (Fig. 8 and 9 are the same as in the preliminary paper, but Fig. 7 is new with the exception of *A*.)

My former description of the second division seems adequate, and as I have nothing new to add, I will quote it as there described.

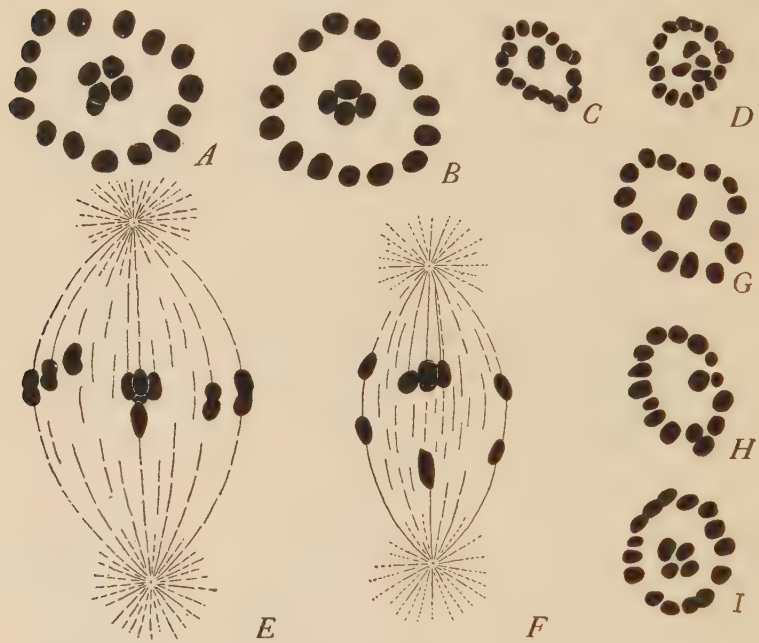


FIG. 8. *Galastocoris* (*Galgulus*) *oculatus* Fabr. *A* and *B*, metaphase figures of the second spermatocyte division, polar view, showing the ring of 15 chromosomes and the pentad group in the center—in *B*, the chromosome beneath the four group could not be shown without displacing it; *C* and *D*, late anaphases of the second division, polar view, showing the unequal distribution of the chromosomes; *E*, side view of the second division, metaphase, showing the typical arrangement and position of the pentad group; *F*, side view of the early anaphase, second division, showing the manner in which the chromosomes of the pentad group separate—the spindle in both *E* and *F* is diagrammatic; *G*, *H* and *I*, early anaphases of the second division. All drawings are made on the same scale and magnified 3,105 diameters.

"The second division which follows immediately after the first, shows a remarkable regrouping of certain of the chromosomes.

Fifteen of the 20 take up the position of a ring, within which is a definite compound element formed by the remaining five. These are now arranged in a pentad group, which always shows the same composition and occupies the same position. Four of these five chromosomes are grouped very closely together and lie in one plane, while the other one is either above or below this group of four, lying close to them on the other side of the equatorial plane (Fig. 8, *A*, polar view of the equatorial plate; Fig. 8, *E*, and Fig. 9, *C*, side views). The 15 chromosomes in the ring divide equally, while the chromosomes of the central pentad do not divide individually, but the group as a whole separates in such a manner that one chromosome passes to one pole and the other four to the other pole (Fig. 8, *F*, and Fig. 9, *D* and *F*). Two classes of spermatozoa are thus formed, which contain 16 and 19 chromosomes respectively. The early anaphase illustrating these two classes is shown in Fig. 8, *G*, *H* and *I*, and Fig. 9, *B*; the later anaphase in Fig. 8, *C* and *D*."

In my previous paper, I also stated somewhat cautiously that 35 was the number of chromosomes in the spermatogonia, as the count was made in only two cells. Fig. 7, *C* and *D*, shows two new groups and I have counted the chromosomes in several other cells, each case showing the same number. At present, I have, therefore, no hesitation in saying that 35 is the number of chromosomes found in the male cells. The female number (oögonial or follicle cells) is 38 (Fig. 7, *A* and *B*). From these facts it is evident that the reduced female group must contain 19 chromosomes; and that accordingly females are produced upon fertilization by the 19-chromosome class of spermatozoa; males upon fertilization by the 16-chromosome class.

Egg 19 plus spermatozoön 16 = 35 (♂),

Egg 19 plus spermatozoön 19 = 38 (♀).

During the growth period, between synapsis and the formation of the chromosomes preparatory to the first spermatocyte division, a large deeply staining body persists, which is more or less comparable to the nucleolus of the forms previously described. In the preliminary note, I suggested the possibility that this body

contained the five differential chromosomes. Further study has thrown very little light upon the question. Fig. 7, *E*, *F*, *G* and *H*, represents its history as far as I have traced it. *E* shows it shortly after synapsis; *F* gives its typical appearance when the cell has reached its maximum size; *G* represents a stage toward the

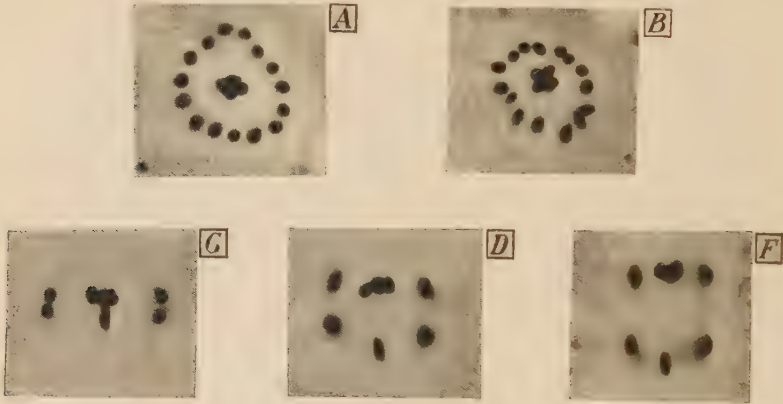


FIG. 9. *Gelastocoris (Galgulus) oculatus* Fabr. *A*, metaphase figure of the second division, polar view, showing the ring of 15 and the four chromosomes of the pentad group near the middle—the fifth chromosome of this group could not be shown, as it lies beneath the four; *B*, early anaphase of the second division, polar view, showing the 19 chromosomes which go to one pole; *C*, metaphase of the second division, side view, showing the typical position and arrangement of the chromosomes of the pentad group; *D* and *F*, anaphases of the second division, side view, showing the manner of separation of the pentad group, four chromosomes of which go to the one pole and one to the other—only three chromosomes of the four group show, as all of them do not lie in the same plane. The photographic enlargement is 1,500 diameters.

end of the growth period and before the chromosomes begin to form. At this time the contents are thrown out into the nucleus and it is probable that the part thrown out is chromatin as it appears to take part in the formation of the chromosome a little later. After the contents are thrown out, the nucleolus does not entirely disappear until the chromosomes are well formed (Fig. 7, *I*). As the five differential chromosomes cannot be identified before the second maturation division, it is impossible to trace their earlier history with accuracy. It is very evident, however, that if they are in the nucleolus they do not come out of it as condensed and separate individuals as they do in the other cases

described. No direct evidence is at hand, yet I still think there is a possibility that the deeply staining body is a plasmosome in which are the five differential chromosomes. While reasoning by analogy may not always be a safe method, the above interpretation, it seems to me, is supported by a comparison of the nucleolus here with those in Fig. 1, *N* (*Diplocodus*), and Fig. 4, *N* (*Conorhinus*). In these two figures the nucleolus stains as intensely black as in *Gelastocoris*, yet it is evident that the differential chromosomes are present, although invisible.

Acholla multispinosa De Geer.

Montgomery has also described in part the spermatogenesis of a form which he called "*Acholla multispinosa*," but according to Van Duzee's identification he was here again mistaken in the species. As previously stated, my figures of the first maturation division, metaphase, in *Acholla multispinosa*, agree in number and size relations with Montgomery's figures of the same stage in "*Sinea*." Again his figures of "*Acholla multispinosa*" agree with my figures of the first division in *Acholla ampliata*. So it seems very probable that the species which he called "*Sinea diadema*" is *Acholla multispinosa*, and that his "*Acholla multispinosa*" is *Acholla ampliata*.

The behavior of the chromosomes in *Acholla multispinosa* is, in several respects, more remarkable than in any of the other species examined. The number of chromosomes in the female cells (Fig. 10, *A*, *B* and *C*) is 30, six of which are much smaller than the others. The male cells (Fig. 10, *D*, *E* and *F*) show 26 chromosomes, one of which is much larger and three much smaller than the remaining ones. At first sight, no evident relation is seen between the male and female groups. A relation becomes evident, however, from a study of the first and second maturation divisions. In the metaphase plate of the first division (Fig. 10, *H*, *I* and *J*) are 16 chromosomes. The three small ones are present and also the large one, which at this time is linked with two other chromosomes, one in contact with each end. This same grouping is present in the prophase of the first division (Fig. 10, *G*). Since there are 26 chromosomes in the



FIG. 10. *Acholla multispinosa* De Geer. A-C, female groups showing 30 chromosomes, six of which are small; D-F, male groups, 26 chromosomes, one of which is very large and three small; G, prophase of the first division showing the chromosome complex; H-J, metaphase figures of the first division with 16 chromosomes—the chromosome complex is still present; K, a side

spermatogonia and 16 in the first division, ten of these must be bivalent and six univalent. While I have not seen the anaphases showing the division of the three small chromosomes, it seems very probable that they and all the others divide equally in this division. The fact that 16 chromosomes are present in the equatorial plate of the second division, supports the above conclusion (Fig. 10, *L*, *M* and *N*; in *L* and *M*, the large chromosome which lies below the five in the middle, could not be shown). The chromosomes in the group of three formed by the large one and two others, lag behind and are the last to divide (Fig. 10, *K*, a side view of the first division, anaphase).

The metaphase plate of the second division again shows a regrouping of the chromosomes, similar in arrangement to those already described, but differing in the number of elements which compose the central group. Ten of the chromosomes form an irregular ring, within which are the other six, forming a hexad group (Fig. 10, *N*), composed of the three small chromosomes, the large one and the two which were linked with it in the first division. The three small and two medium sized ones lie approximately in one plane, while the large one lies a little above or below these five, on the other side of the equatorial plane. Unfortunately no side views of the metaphase showing all six members of the hexad group, were present in my material. The small chromosomes are so very minute at this stage that they are with difficulty seen at all. The chromosomes in the ring divide equally, while the members of the hexad group do not divide individually, but the group separates so that the large one passes to one pole and the remaining five to the other. Anaphases showing a clear demonstration of this separation were not present in my material. If there is any doubt as to the

view of the first division, anaphase, showing the late division of the complex; *L-N*, metaphase figures of the second division, showing the ring of ten bivalents and the univalents in the center—in *M* and *N* only five of the univalents are shown, as the large one lies beneath; *O*, side view of the second division, anaphase, showing the manner of separation of the large and two medium sized univalents—one small one is also present. No anaphases, showing the distribution of the three small univalents, were present. *P*, anaphase, polar view of the second division, showing the two medium univalents, and two of the small ones; *Q*, anaphase, showing the large univalent going to one pole. The enlargement is 4,018 diameters.

manner of the separation, it is in regard to the behavior of the small chromosomes. Fig. 10, *O*, a side view of an early anaphase, and Fig. 10, *P* and *Q*, pole views of the early anaphases, demonstrate clearly the behavior of the large and two medium sized ones. A number of anaphases showing one and two small chromosomes were present (Fig. 10, *O* and *P*), and when present, they were always with the two medium sized ones and not with the large one. A thorough study of many anaphases showing the large chromosome, has in no case, revealed the presence of a small one (Fig. 10, *P*). Further, the number of chromosomes and their size relations in the male and female cells makes it almost conclusive how the hexad group separates. As previously stated, the female group has 30 chromosomes, six of which are very small, and the male group has 26, three of which are small and one very large. If five members of the hexad group go to one pole and one to the other, two classes of spermatozoa are produced, containing 15 and 11 chromosomes respectively. The 15-chromosome class will contain 12 chromosomes of nearly equal size and three very small ones. The 11-chromosome class will contain ten chromosomes of approximately equal size and one very large one. Now, if the 15-chromosome class meets an egg with 15 chromosomes, three of which are small, the cells of the resulting individual will have 30 chromosomes, six of which will be small. This condition is fulfilled in the female chromosome group. If the same egg is met by the 11-chromosome class of spermatozoa, the cells of the offspring will contain 26 chromosomes, three of which will be small and one very large. This is the number and size relations found in the male cells. No other manner of separation of the hexad group could bring about a similar end result. It becomes evident then that the reduced number of chromosomes in the egg is 15, and that females are produced upon fertilization by the 15-chromosome class of spermatozoa; males upon fertilization by the 11-chromosome class.

Egg 15 plus spermatozoön 11 = 26 (♂),

Egg 15 plus spermatozoön 15 = 30 (♀).

As previously stated, the material which I have, does not

justify me in saying that the above statements are absolutely true, but all the data point in that direction. I hope to reëxamine the form as soon as material can be procured. If, then, these inferences prove true, *Acholla multispinosa* gives another new type of chromosome distribution in which the female has four more chromosomes than the male. For lack of material, I have not attempted to follow the differential chromosomes through the growth period.

It was noticed in the prophase and metaphase of the first division that three chromosomes (the large one and two others) were joined together end to end. Montgomery described such a complex in his account of the chromosomes in a species which he called "*Sinea diadema*." In his first paper ('01) he considered the large chromosome representing two bivalents, but later ('06) described it as one large bivalent. All three members of this complex prove to be univalent in *Acholla*, since they divide only in the first mitosis.

In all previous cases where a dimorphism of the spermatozoa in regard to the number of chromosomes exists, the female has not only received the larger number of chromosomes, but as far as we can judge with the eye, the larger amount of chromatin. While the numerical rule still holds, *Acholla* seems to give an exception in that the quantity of chromatin which goes to the male-producing pole is greater than that which goes to the female-producing one. I have made a number of measurements in the first and second divisions, and in every case, the large chromosome seems to contain a larger amount of chromatin than the remaining five differential chromosomes. In connection with the question of sex-determination, this point will be discussed further.

What can be the significance of such a chromosome complex as is present in the first maturation division and in the prophase of this division? In the Phasmidæ, Sinety ('01) recorded a coupling of the odd chromosome with one of the ordinary bivalents. McClung ('05) extended this observation to two other families of Orthoptera, the Acrididæ and Locustidæ. Wilson ('07) describes a coupling of the supernumerary chromosome with one of the idiochromosomes in *Metapodius* and suggests the possibility that such chromosome couplings may give

the physical basis of certain forms of correlation in heredity. The suggestion seems a very plausible one for the above cases, but the complex in *Acholla* is somewhat different. All three chromosomes are univalent and divide in the first division. In the second division the group separates, the large chromosome passing to one pole and the other two to the opposite pole.

Acholla ampliata Stal.

Acholla ampliata appears to be the species which Montgomery ('01 and '06) describes under the name of "*Acholla multi-spinosa*." He figures the spermatogonial division with 32 chromosomes, eight of which are very small, and both the first and second divisions with 16 chromosomes, four of which are small. In the first division, the four small ones may lie in any position, but in the second division, they are centrally placed and grouped closely together. Unfortunately my material shows only the first and second divisions which agree with those, which Montgomery figures, except that in the second division, the small ones are grouped so closely together that it is impossible to distinguish



FIG. 11. *Acholla ampliata* Stal. A and B, metaphase figures of the first division, 16 chromosomes; C and D, metaphase figures of the second division—there are 12 chromosomes in the ring and the small ones are grouped in the center so that it is impossible to count them; E, typical appearance of the nucleus during the later part of the growth period—the four small chromosomes are embedded in the plasmosome; F, prophase of the first division—the plasmosome has disappeared, but the four small chromosomes remain. The enlargement is 4,018 diameters.

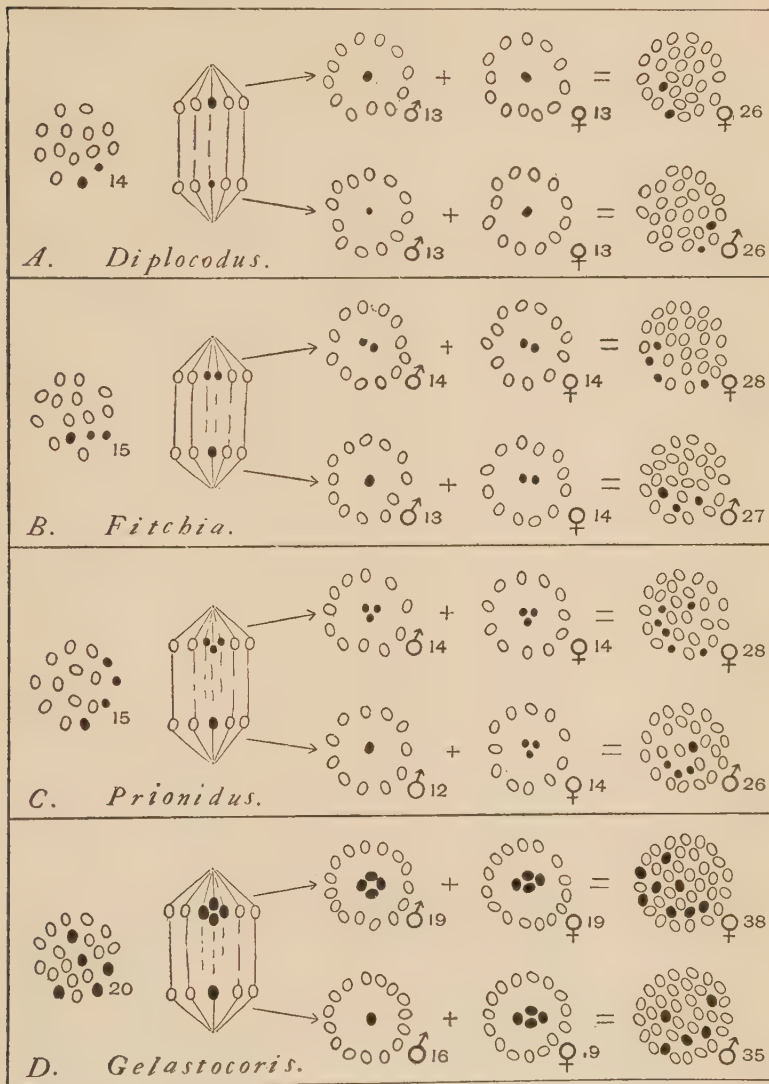
Polar view of
the first
division
metaphase.

Side view of
the second
division
anaphase.

Two classes of
spermatozoa.

Reduced number
of chromosomes
in the egg.

Male and female
chromosome
groups.



the number or arrangement with certainty. This difference, however, could be easily accounted for by a difference in fixation, as I have noticed the same thing in regard to the tetrad group in *Sinea*. As he found 32 chromosomes in the spermatogonia, Montgomery thought that the four small ones divided equally in both divisions, and he figured them as dyads attached to the plasmosome during the growth period. I have no evidence to offer to the contrary, but one thing comes out clearly in a study of the growth period, and that is that the four small chromatin bodies which Montgomery calls "chromatin nucleoli," show no appearance of being bivalent, and that they are not merely in contact with the plasmosome, but are actually embedded in it (Fig. 11, *E*). In the prophase of the first division (Fig. 11, *F*), the plasmosome breaks down and the small chromosomes remain, but even here they do not appear to be bivalent.

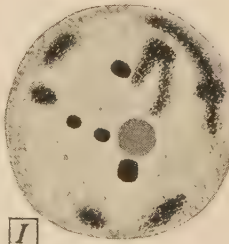
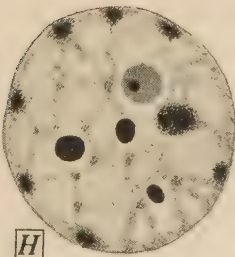
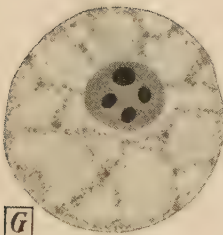
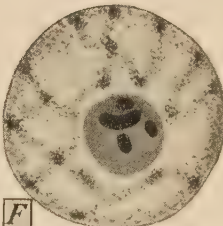
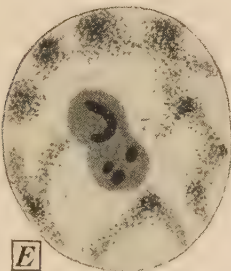
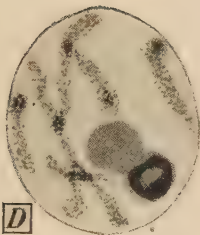
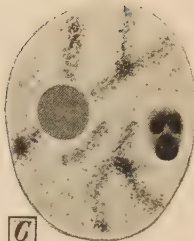
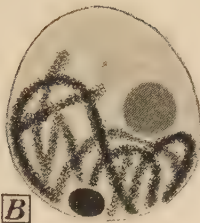
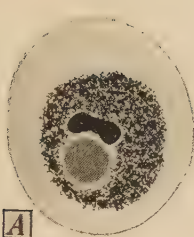
In comparing Fig. 11, *E* and *F*, with Fig. 6, *M* and *N*, the same stages in *Sinea diadema*, we notice a striking similarity. As the four small chromosomes embedded in the plasmosome in *Sinea* are univalent, is it not also possible that the same is true in *Acholla*? In the light of the present discoveries, it seems desirable that the form be reëxamined.

In order to summarize briefly the results, I have made a diagram (Fig. 12) illustrating the four different types of chromosome distribution described in the present paper. I have omitted from the diagram the type described in *Acholla multispinosa* as my evidence is hardly conclusive. The differential chromosomes are in each case made in black, while the remaining ones are left in outline. The size relations of the differential chromosomes are maintained as nearly as possible. In the first column to the left, are the metaphase figures, polar view, of the first division in each type. In the second column are side views of the second division, anaphase, showing the manner of separation of the dyad, triad, tetrad and pentad groups of differential chromosomes. The third column gives the two classes of spermatozoa produced in each type; the fourth, the reduced number of chromosomes in the egg (inferred); and the fifth, the end result produced by the fertilization of the egg by the two classes of spermatozoa.

(To be continued.)

EXPLANATION OF PLATE I.

Prionidus cristatus Linn. These drawings illustrate the history of the differential chromosomes and the plasmosome during the growth period. *A*, about the contraction-phase of synapsis—the plasmosome and a deeply staining chromatic body is present; *B*, the spireme stage following synapsis; *C*, the chromatic body is breaking up and a plasmosome is forming around it; *D*, the stage following *C*—the two plasmosomes have commenced to fuse; *E*, the chromatic element breaks up for the first time into its constituent elements, the differential chromosomes; *F* shows the complete fusion of the two plasmosomes; *G* gives the typical appearance of the plasmosome and differential chromosomes during the greater part of the growth period—the larger differential chromosome has contracted; *H*, a prophase of the first division—the plasmosome has grown smaller and the differential chromosomes are coming out; *I*, prophase of the first division, where all the differential chromosomes have left the plasmosome. *A*, *B*, *C*, *D* and *E* are enlarged 4,018 diameters; *F*, *G*, *H* and *I*, 2,594 diameters.



SOME NEW TYPES OF CHROMOSOME DISTRIBUTION AND THEIR RELATION TO SEX. *Continued.*

FERNANDUS PAYNE.

GENERAL.

The Chromosome Nucleoli.

The term "chromosome nucleolus" has come to mean, in a general sense, any chromosome, which remains condensed during the growth period. Under this heading, then, I shall discuss briefly the origin, valence and history of four different classes of chromosomes, namely: the accessory chromosome, idiochromosomes, m-chromosomes and differential chromosomes.

Henking ('91) observed a deeply staining body in the growth period of the primary spermatocytes of *Pyrrhocoris*, but did not detect its origin. He did recognize its chromatic nature and its unequal distribution in the second division, whereby one spermatozoön received one more chromatin element than the other. Montgomery ('98) was the first to detect that the accessory chromosome (chromosome nucleolus) was nothing more than a spermatogonial chromosome which differs in its behavior from the others, but he believed that it divided in both divisions. Paulmier, in his work on *Anasa tristis* ('99) described an accessory chromosome or what he called a "chromatin-nucleolus," which he thought originated at the time of synapsis by the union of two small spermatogonial chromosomes, divided in the first maturation division, but passed over undivided in the second. Montgomery ('01) discarded his former interpretation and accepted that of Paulmier. In the case of *Syromastes* ('04) and *Pyrrhocoris* ('06), Gross believed the accessory chromosome to arise by the fusion of two spermatogonial chromosomes which

divided in one division but not in the other. According to these interpretations, then, the accessory chromosome would be bivalent.

McClung, however ('01), maintained the accessory to be univalent. Wilson ('05 and '06) has shown in the Hemiptera heteroptera that Paulmier ('99) and Montgomery ('01) were wrong in their interpretation of the origin of the accessory chromosome, that the small bivalent divides in both divisions, and that the accessory chromosome is a univalent spermatogonial chromosome which divides in only one division, and this was confirmed by Montgomery ('06) in opposition to his earlier conclusion.

The results of Gross ('04 and '06) have been more or less of a hindrance to the correct interpretation of the accessory chromosome. Wilson ('09) again has shown that Gross was mistaken in the case of *Pyrrhocoris* and that the accessory chromosome is here univalent. He confirms, however, Gross's results on the male cells of *Syromastes*. The spermatogonial number is even (22), and the accessory chromosome is here, in fact, bivalent, but it divides in only one division. Gross figured the same number of chromosomes in both male and female cells, but Wilson inferred (not having material) that the oögonial cells would show 24 chromosomes, since the accessory chromosome is bivalent. In an addendum to his last paper ('09b) Wilson states that his inference has proven true and that the female cells of *Syromastes* have, in fact, 24 chromosomes. In principle, therefore, *Syromastes* conforms to those forms in which the accessory chromosome is univalent.

Another contradiction occurs in the work of Foot and Strobell ('07) on *Anasa tristis*, who assert that the densely staining body in the rest stages of the spermatocytes is a true nucleolus and not a chromosome nucleolus formed by the accessory chromosome as described by Wilson ('05 and '06) and Montgomery ('06). Wilson's reëxamination of his preparations with additional studies on smear preparations and living material, led to the same conclusion as before. Lefevre and McGill ('08) have reëxamined the form and their results agree in every detail with those of Wilson and the later ones of Montgomery. From the

evidence at hand, there seems to be no doubt that Foot and Strobell were in some manner misled.

Boring ('07), in 22 species of Hemiptera homoptera, describes the accessory chromosome as univalent and dividing only in the second division.

The work of McClung, Sinety and Sutton on the Orthoptera, has been consistent in showing that the accessory chromosome arises from a single spermatogonial chromosome. In apparent contradiction to this interpretation are the results of Voinov ('04) on *Gryllus*, Montgomery ('05) on *Syrbula* and Zweiger ('06) on *Forficula*. Each of these observers describe the accessory chromosome as arising from the fusion of two spermatogonial chromosomes and dividing in both divisions. In opposition to Montgomery's work on *Syrbula* is the recent paper by Robertson ('08) on the same genus. He seems to demonstrate conclusively that the accessory chromosome is univalent and divides in only one division. Randolph ('08) in the earwig *Anisolabis*, describes an equal pair of idiochromosomes. May it not be possible that Zweiger mistook, in *Forficula*, such a pair of idiochromosomes for a bivalent accessory?

Montgomery ('05) also described the accessory chromosome of *Lycosa*, a spider, as bivalent and arising from the union of two spermatogonial chromosomes. While he did not determine definitely the manner of its division, he was inclined to believe that it divided in both divisions, judging from the manner of its formation. About the same time Wallace ('05) published her account of *Agalena*. She figured two accessory chromosomes which divided in neither division. In an attempt to unravel these contradictions, Berry ('06) describes the behavior of the chromosomes in *Epeira*. She shows conclusively that there is an odd number of chromosomes in the spermatogonia and that the accessory chromosome is a spermatogonial chromosome which retains its identity throughout the growth period and divides in only one division. This makes the results in spiders consistent with the majority of those in the Orthoptera and Hemiptera.

The results of Blackman on *Scolopendra* ('05) and Medes on *Scutigera* ('05) show that the accessory chromosome in the Myriapoda is a single spermatogonial chromosome, but each finds

the chromosome nucleolus of the growth period ("Karyosphere") made up of all the chromosomes.

McGill in her earlier work on *Anax junius* ('04) described the accessory chromosome as arising from a union of two small chromosomes as Paulmier had done in the case of *Anasa tristis*. The later paper of Lefevre and McGill ('08) on the same form, corrects the above error and shows that the accessory chromosome is a single spermatogonial chromosome.

The accessory chromosome in the Coleoptera as described by Stevens ('05, '06 and '09) arises from a spermatogonial chromosome and divides only in one division.

The idiochromosomes as described by Wilson ('05 and '06) for the Hemiptera, Stevens ('05 and '06) and Nowlin ('06) for the Coleoptera, and Stevens ('08) for the Diptera, are two univalent spermatogonial chromosomes which usually remain condensed throughout the growth period. They unite at synapsis in the Coleoptera and one chromosome nucleolus is present during the growth period except in *Tenebrio*, where the idiochromosome bivalent does not remain condensed. In the Hemiptera and Diptera they may or may not unite at the primary synapsis to form a bivalent body. In the former case, one chromosome nucleolus is present during the growth period, but separates into its univalent elements before the first maturation division. In the latter case, two chromosome nucleoli are present in the growth period.

The m-chromosomes as described by Wilson ('05), are two spermatogonial chromosomes which do not unite at the general synaptic period and which may or may not condense in the early growth period to form two small chromosome nucleoli. They undergo a late synapsis in the prophase of the first division to form a bivalent, which divides in both divisions.

We thus see that the three classes of chromosome nucleoli—namely, those derived from the accessory chromosome, from the idiochromosomes, and from the m-chromosomes, are alike in that all are direct descendents of spermatogonial chromosomes.

The differential chromosomes or chromosome nucleoli of the Reduviidæ, which are described in the present paper, are in each case, with the possible exception of *Acholla ampliata*, univalent,

and derived from univalent spermatogonial chromosomes. The case of the large nucleolus of *Gelastocoris* is not so clear, but as previously stated, there is a possibility that the differential chromosomes are embedded in the nucleolus, although not as distinct and separate individuals as in the Reduviidæ. The differential chromosomes in the Reduviidæ, are without exception (as far as examined) embedded in a plasmosome. This plasmosome may be pale (*Prionidus*, *Sinea*) in which case the chromosomes stand out clearly, or it may stain rather densely (*Diplocodus*, *Conorhinus*) so that the chromosomes can be seen only faintly or not at all. In this respect they differ from the chromosome nucleoli formed by the accessory, m- and idiochromosomes. The accessory chromosome is, in the early part of the growth period, in contact with a pale plasmosome, but later separates from it. The idiochromosomes also may be associated during a part of the growth period with a plasmosome. The m-chromosomes may lie in any position and have no relation to the plasmosome.

Origin of the Differential Chromosomes.

In a study of the differential chromosomes, one of the most interesting questions which arises, is the origin of the asymmetrical chromosome distribution. It seems almost a certainty that these peculiar forms of distribution have not been present since the origin of the species, but have arisen sometime within its history.

In a discussion of this question, Montgomery ('06) is inclined to the belief that the m-chromosomes and idiochromosomes are not radically different structures, but are rather extremes of a series of modifications. Of their origin he says, "First a pair of autosomes (chromosomes) became modified so as to retain their compact nature during the growth period, still maintaining their approximate equivalence in volume. Because such autosomes are usually very small, we might conclude also, that they arose from the smallest pair of autosomes. In the next change would appear a growing disparity in size, which, if our last assumption be correct, would be due not to one becoming smaller and the other becoming larger, but rather to one retaining its original volume and to the other becoming much larger. This

second step would then be one of differentiation of the two, a becoming different, probably implying also difference of metabolic activities. This would account for the lessening affinity of the two as exhibited by the protraction of the time of conjugation. Then would be attained the stage of the second type of diplosomes (idiochromosomes), no longer united but separate in the first maturation spindle. And the last step would be that, instead of a reduction division of them in this spindle there would take place there an equational division of each." This conception is rendered untenable by Wilson's discovery that in *Metapodius* a typical pair of m-chromosomes and of unequal idiochromosomes coexist in the same species. In his papers of '01 and '05, Montgomery has argued that the accessory chromosome is bivalent and arose by some abnormality in mitosis as by the failure of two spermatogonial chromosomes to separate. Wilson ('05 and '06) suggests that the accessory chromosome may have arisen by the gradual disappearance of the small idiochromosome. Montgomery ('06) realizes this possibility, although he offers objections to it. While Wilson still believes that this interpretation may be applicable in many cases, in his work on *Metapodius* ('09b), he gives another possibility of its origin along with that of the supernumeraries. He says, "This was suggested by the observation that in a very few cases in 22 chromosome individuals, both idiochromosomes were seen passing to the same pole in the second division. The rareness of this occurrence shows that it is doubtless to be regarded in one sense as abnormal. But even a single event in an original 22-chromosome male, if the resulting spermatozoa were functional, might give the starting point for the whole series of relations observed in the genus, including the establishment of an unpaired idiochromosome. The result of such a division should be a pair of spermatozoa containing respectively 10 and 12 chromosomes. The former might give rise at once to a race having an unpaired idiochromosome and the somatic number 21 in the male. The latter might similarly produce an individual having in the first generation a single supernumerary chromosome and in succeeding generations an additional number."

In regard to the possible origin of the supernumeraries in

Diabrotica, where they are associated with an odd chromosome instead of a pair of idiochromosomes, Stevens ('08) makes the following suggestion: "It may be possible, as was surmised earlier in the study, that (1) there will prove to be two distinct types (varieties or species), in each of the present species, one having the large unpaired heterochromosome only; the other having an equal pair of chromosomes as in *Haltica*, and that (2) the irregularities in time of division and the consequent peculiarities in number and distribution of the supernumeraries in *Diabrotica* are to be attributed to hybridism."

The differential chromosomes in *Gelastocoris* and in the Reduviidæ seem to have undergone a somewhat different history from that of the other types. It is clear that the single large idiochromosome of *Diplocodus* is represented in *Fitchia* by two chromosomes, in *Prionidus* and *Sinea* by three and in *Gelastocoris* by four chromosomes. It is very probable that the condition seen in *Diplocodus* is the most primitive one, and the essential question is how the other types can have been derived from this. Taking as an example *Fitchia*, where the female number is 28 and the male 27, if a pair of idiochromosomes was the original condition in the species, the original number of chromosomes must have been 26 in both male and female. If, in the male, the original large idiochromosome should break up into two parts, two classes of spermatozoa would be found, one containing 13 chromosomes and the other 14. All the eggs would have 13 chromosomes. If an egg were fertilized by a 14-chromosome class of spermatozoa, the result would be a female with 27 chromosomes. In maturation, this female would produce two kinds of eggs, one with 14 chromosomes and the other with 13. The 14-chromosome class fertilized by a spermatozoön with 13 chromosomes would produce either a male or female with 27 chromosomes. From these individuals, then, would arise both eggs and spermatozoa with 13 and 14 chromosomes. As the 14-chromosome class of spermatozoa would be female-producing, females with 28 chromosomes would be produced upon fertilization of an egg with 14 chromosomes by a spermatozoön with 14 chromosomes. Further, an egg with 14 chromosomes, fertilized by a spermatozoön with 13 chromosomes would produce a male with

27 chromosomes. This gives the number relations as we find them at present if the individuals with the original number (26) and the females with 27 disappear. The same explanation holds for the remainder of the types if we assume that the large idiochromosome breaks up into three or four elements instead of two. Another thing which adds weight to the above interpretation is the fact that the behavior of each of the triad, tetrad and pentad groups, as a whole, is exactly comparable to the behavior of a pair of idiochromosomes. Evidently the original irregularity might have first occurred in either sex and have been transferred to the other. This gives another method by which the chromosome number may change during the history of the species. While *Metapodius* and *Diabrotica* are species where a change is actually taking place at the present time, the forms described in the present paper (with the exception of *Diplocodus*) show a fixed condition after a change has taken place.

Sex Determination.

In a preliminary note ('08) Morgan has given some interesting data in regard to sex determination in phylloxerans, where all the fertilized eggs produce females and where both males and females develop from parthenogenetic eggs. In describing the spermatogenesis he says: "The reduced number of chromosomes is three. In the first spermatocyte division two of these divide equally, but the third lags behind the others, and finally in the very last stages of this division, it retreats to one of the poles. Thus there are three chromosomes in one of the two daughter cells, and only two in the other. Still more significant is the fact that the cell with the fewer chromosomes is very small; it contains very little cytoplasm and subsequently degenerates without forming a spermatozoön. In the second spermatocyte division all three chromosomes of the larger cell divide equally, thus producing two spermatids with three chromosomes each. These spermatids become spermatozoa. They correspond in their mode of development to the 'female-producing' spermatozoa of other insects. Hence we can understand why all fertilized eggs become females."

To those who have sought to bring forward a theory of sex

determination of universal application, the parthenogenetic forms have been more or less of a stumbling block. The above results are in perfect harmony with the hypothesis of sex-production advocated by McClung, Stevens and Wilson.

Morgan also gives some further observations, indicative as to the manner in which males and sexual females are produced from parthenogenetic eggs. "I find that the somatic cells of the males of the species referred to above contain only five chromosomes. These five give in the spermatogenesis the reduced number three by two uniting with each other and the third having no partner. I find that the somatic cells of the female contain six chromosomes. It follows that at some time in the life cycle of the parthenogenetic eggs, one chromosome disappears in those eggs that become males, while the full number is retained in the female. It seems plausible that this change takes place in the formation of the single polar body given off by the parthenogenetic egg.

"The results seem to show that while the sex of the stem mother is connected with the presence of 'female-producing' spermatozoa, the production of males and of sexual females is dependent on a process that takes place in the egg analogous to the same process that takes place in the spermatogenesis of other kinds of insects. Hence it follows that the egg as well as the sperm has the power of determining sex by regulating the number of its chromosomes."

Von Baehr's recent results ('08) and also those of Stevens ('09) on the aphids confirm those of Morgan on the phylloxerans.

In a preliminary note ('08) Baltzer gives some results on echinoderm eggs, where he finds in the early cleavage stages of fertilized eggs of *Echinus microtuberculatus* and *Strongylocentrotus lividus*, an unpaired element which comes from the egg nucleus. Further, this unpaired element is present in only a part of the eggs. He suggests the possibility that this may be a chromosome which has to do with sex determination. If this element should prove to be a chromosome and in one half of the eggs, it would be the reverse of the condition found in the insects, for there the unpaired chromosome has arisen in the male. However, two such diverse phenomena are not impossible in different groups of animals, as we have no reason to suppose that

sex differentiation has taken place in the same manner in all animals. In fact, the quotation from Morgan shows that two classes of eggs are produced in phylloxerans and that the inequality of the chromosome distribution is accomplished in some manner at the time of the formation of the polar body.

McClung, Stevens and Wilson in their studies on the chromosomes of the insects have argued that the accessory chromosome and the idiochromosomes are either sex determinants or are in some manner connected with the determination of sex. The manner in which this is brought about yet remains a question. Wilson ('06) gives two interpretations by which the end result as we find it may be reached. First he follows out the earlier hypothesis of Castle ('03) that sex production may be interpreted as the result of a Mendelian segregation, transmission and dominance of the sexual characters. This interpretation involves two assumptions, neither of which have been proven, but which he argues may not be insuperable difficulties. One is the assumption that there are two kinds of eggs, the other, that selective fertilization occurs.

As an alternative point of view, he gives a second interpretation, in which he suggests that possibly the differential chromosomes may not be qualitatively different except in the degree of their special activity; or the end result may be due merely to a quantitative difference in the chromatin. Wilson, himself, in his work on *Metapodius* ('09), where the female may or may not have a larger amount of chromatin than the male, has brought forward evidence against the quantitative interpretation.

My results in the present paper offer nothing new in regard to the theory of sex determination, but are in perfect accord with the majority of previous results on the insects. I shall not venture far into theoretical discussions. There is, however, one question which naturally arises. Why do we have so few as one and two chromosomes involved in the production of males and females respectively in those forms with an odd chromosome, and as many as five and eight in *Gelastocoris*? This is not so strange, if the unequal distribution in these forms has arisen from a pair of idiochromosomes as previously explained. In every case whether the difference in number be one, two, three

or four, the female has the larger quantity of chromatin with the possible exception of *Acholla multispinosa*. Here the male seems to have the greater quantity and this inequality is brought about by the differential chromosomes themselves. This argues further against the interpretation that sex is determined by a quantitative relation of the chromatin.

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